ON THE BREEDING HABITS OF DESMOGNATHUS FUSCA.

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That the eggs of *Desmognathus fusca* are deposited under terrestrial conditions, and are brooded by the mother during their development, are facts already well known. In my account of the "Life History of *Desmognathus fusca*" (I. W. Wilder, '13), I made the following observation and suggestion: "The eggs are always found guarded by a female, undoubtedly the mother. She usually so places herself among them as to bring practically all of the eggs in contact with her body, which often extends through the mass of eggs and is frequently bent sharply upon itself as if the better to surround and protect them (Fig. 1).

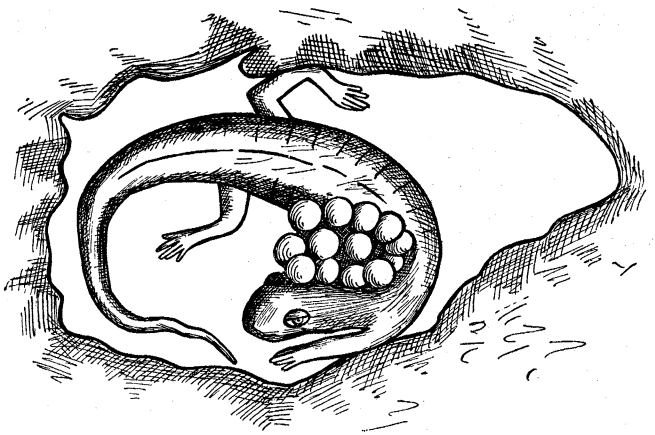

FIG. 1. Female *Desmognathus fusca* with eggs, showing the characteristic brooding position, with the body coiled about the eggs. Drawn from life by H. H. Wilder. From *American Naturalist*, Vol. XXXIII.

When under observation, as in a terrarium, the mother frequently leaves the eggs when disturbed, always retreating through the same exit from the nest. After having been separated from the

eggs, however, as may occur in making a transfer from out of doors to the laboratory, the mother goes back to them again, even though the nest and all of its surroundings may have been reconstructed. I have never had the opportunity to further test the sense of ownership of eggs in a mother by exchanging the eggs of two individuals, but the experiment would certainly be an interesting one."

In connection with later experiments upon the mating habits of *Desmognathus fusca*, certain facts have come under my observation which give more definite information concerning this brooding instinct of the mother and her behavior during the brooding period. These facts furnish, in addition, more exact data concerning the length of the incubation period of the species, which, at the time of the publication of my account, was not definitely known.

On July 2, 1915, late in the afternoon, a female *Desmognathus fusca* which had been under observation in the laboratory since May 20, 1915, confined in a terrarium with another gravid female and a male, was found to have deposited a batch of eggs. These had been laid within the previous twenty-four hours, and were in the early segmentation stages when found. The companion male and female were immediately removed from the terrarium and in order to make sure that the eggs were actually those of the female with whom they had been found associated, the companion female was examined and found to be still gravid.

The terrarium in which the eggs were laid was a rectangular glass one, measuring 13 inches long by 8 inches wide by 13 inches deep, and had a two-inch layer of wet sand in the bottom, sloping down at one corner to allow the water to stand in a shallow pool. Upon the sand had been placed wet sphagnum moss, and a stone about 4 inches in diameter was lying upon the sphagnum near the end of the terrarium which was opposite to the pool. It was in a cavity in the sphagnum underneath the stone that the eggs, 22 in number in two clusters, were found with the mother coiled about them in the usual brooding position of the species.

During the subsequent weeks the stone was frequently lifted to examine the nest, in the evening as well as during the

daytime, and the mother was always found in this characteristic coiled attitude, although the relative position of the eggs and the mother was slightly changed from day to day. She seemed little disturbed by these brief examinations unless the eggs were actually handled, when she would leave the nest and go away a little distance, always, however, to return to her charge later. On August 23, after an incubation period of 52–53 days, the eggs began to hatch, the process continuing through August 25.

Meanwhile, on July 7, in the late afternoon, another female in a similarly arranged terrarium, was found to have begun to deposit eggs. This female had been captured on the same date as the first (May 15), had shown when captured a similar evidence of the presence of ripe eggs conspicuous through the body wall, and had been similarly confined since May 20 with another gravid female and a male. On July 1 the male had been removed, however, and as soon as the eggs were discovered the other female was removed also. At this time a small cluster of three or four eggs had been deposited, and a single isolated one which was removed at once from the nest for examination, and was at this time unsegmented.

On the following forenoon the egg-laying process had been completed, and the usual two clusters of eggs were found, one numbering six and the other twelve. The cluster of six eggs was appropriated for study of the early cleavage, and it was found that at that time, about twelve o'clock, some of them were in the first cleavage stage, while others showed as yet no suggestion externally of the cleavage process. The one which had been removed on the previous afternoon was at this time in the second cleavage stage.

The eggs of this second batch were deposited in a cavity hollowed out in the moist sphagnum under the stone, as was the case of the first batch of eggs which had been deposited in the other terrarium a week earlier. This second mother, however, took from the beginning an unusual position with reference to the eggs, for instead of lying among them with her body coiled about them, she stood over them with her body in a straight line and slightly elevated so that the eggs were beneath her belly and only slightly in contact with it. Care was always taken in

examining the nest not to disturb her or her surroundings beyond lifting the stone carefully from the nest and replacing it with equal care, in exactly the same position. She was invariably found in the same peculiar attitude with relation to the eggs, and always with the head oriented in the same direction.

On August 24, after the eggs of the first batch had begun to hatch, both of the mothers were removed from their respective eggs. The mother of the second batch was killed and preserved. The mother of the first batch, now hatching, was transferred to the terrarium containing the second batch, now motherless, but was placed in the part of the terrarium farthest from the stone under which the eggs were located. Great care was taken to leave the sphagnum surrounding the eggs, and the stone covering them in the same relative position which they had had throughout the incubation period.

On the following day when the terrarium was examined the female was not in sight, but upon lifting the stone, she was found under it brooding the eggs and standing over them in exactly the same unusual position which their own mother had habitually assumed. She remained with them and was always found in the same position, with her body oriented in the same direction, until, on September 2, a week later, all of the eggs had hatched. Upon this date the young were found clinging to the body of their foster mother as she stood with her customary orientation, a number of them surrounding the middle of her body like a rosette, with their long axes parallel to hers but with their heads pointing in the opposite direction. When she was disturbed, a few were somewhat scattered while most of them still clung to her body. After a few days, the adult was found in the little pool at the opposite end of the terrarium, and the young, still in the terrestrial larval stage, were distributed through the moist sphagnum between the nest and the pool.

Of course there is no means for determining whether the actual finding of the eggs by the foster mother was a reaction to the proximity of the eggs themselves, or was a purely accidental occurrence, since *Desmognathus* frequently seeks out positions under stones and other objects lying upon the surface. Obviously, however, in her subsequent week of continual brooding

of the eggs, and in her assumption of the very unusual attitude during this period, we have an interesting example of a perfectly automatic response to external conditions. Otherwise her attitude would hardly have shown, as it did, so exact a correspondence to the aberrant one previously assumed by their own mother, but would rather have been the characteristic one which the foster mother had taken in brooding her own eggs. The chief of the conditions controlling this automatic response would seem to have been the presence of the eggs themselves, since, after the foster mother had once reached the pool, she apparently did not return to the stone again but was always found in or near the pool. The peculiar position and orientation of the bodies of the two females while successively brooding this particular batch of eggs is most satisfactorily explained, however, as a response to some unusual conditions in the surroundings of the nest, such as the possible entrance of a little light into the nest from one direction. This explanation receives some corroboration in the fact that a little crevice was noted leading from the surface into the side of the nest toward which the head of the adult was directed. Furthermore, the newly hatched larvæ, which would be expected to be negatively phototropic if they are to succeed in reaching the neighboring water by working their way down through the moist earth and debris, oriented themselves in the direction opposite to that of the mother.

It is moreover possible that we have a further automatic response exhibited by the mother in seeking the water after the young had hatched. This movement toward the water would be of use to the offspring, for they tend to cling to the mother and would thus be eventually guided by her to the water. Under natural outdoor conditions where the nest would be farther away from the water than was possible within the limited dimensions of the terrarium, the time occupied in making this transfer might roughly coincide with the duration of the terrestrial larval stage.

That the terrestrial larval stage is really a definite one is shown by the behavior of the newly hatched larvæ when placed in the water. They are so well developed muscularly that they can not only swim, but can maintain a horizontal position in the

water when not swimming, instead of lying on one side as do the newly hatched larvæ of most amphibians. Nevertheless they will not remain in the water, but persistently crawl out and lie, often in a mass together, in the moist debris along the edges. It is not until all external evidence of the yolk mass has disappeared that they will remain in the water.

The period of incubation in both of these broods was approximately eight weeks (53–55 days in the first case, and 56–57 days in the second), a considerably longer time than that previously estimated by me, which was five weeks. The terraria were kept in a cool basement room, where the temperature did not vary much from 21° C. (70° F.), which was probably somewhat above the average temperature to which the eggs would have been subjected under natural conditions along the banks of brooks in shaded ravines. The former estimate of five weeks was based upon observations of a batch of eggs which were deposited and developed under still warmer laboratory conditions. As the measurements and descriptions of an embryo from this batch after 30 days' development (H. H. Wilder, '99) show a considerably larger size and a more advanced stage of development than the 34 day embryos of the batch of eggs here reported, one is justified in the conclusion that at the higher temperature development took place more rapidly. On the other hand, it is conceivable that in nature the period of incubation might easily be prolonged to more than eight weeks by the lower temperature to which the eggs would certainly be subjected in the neighborhood of cold, spring-fed, mountain brooks. Thus the batch of eggs previously described by me as having been found in nature hatching on September 24 (I. W. Wilder, '13), after an unusually cool summer, may even have been deposited as early as the middle of July, the month reported by Reed and Wright ('09) as the month of maximum egg-laying for the species. This longer estimate of the period of incubation under natural conditions would account for the usual absence of the larvæ of this species from the brooks during the summer months, a fact which is reported by my colleague, Mr. E. R. Dunn, in an article now in press.

The female which acted as the foster mother in the case here

reported was continued under observation in the laboratory for nearly a year. She was fed abundantly upon *Drosophila*, which, as a "by-product" of genetics experimentation, has proved a valuable laboratory food for adult salamanders. In spite of her well-nourished condition, however, she gave no evidence of the ripening of a new lot of eggs during the following spring and summer, while another female of about the same size (87 mm. in total length), which had not been gravid the previous year, developed under the same care and feeding, large eggs which could be conspicuously seen through the body wall early in the spring. These observations are too limited in number to base any definite conclusions upon them, but they at least suggest that the females of this species do not necessarily produce eggs every year. This hypothesis would also explain the fact that I have found that occasionally females collected in early spring contain no large eggs. The number of offspring in this species is in any case very limited, as shown by the small number of eggs in a batch. These average about 20 in the cases which have come under my observation in western Massachusetts, while the largest number of ripe eggs which I have counted in the ovaries of a single individual is only 28, and the number in a batch may run as low as 14. If in addition to this characteristically small number of eggs produced at a time, the females sometimes fail to produce eggs every year, there would be a still further limitation in the number of offspring. Such a reduction has been made possible only by the high percentage of success in the development of the few eggs which are produced. One of the conditions contributing largely to this success is the large amount of yolk present in the egg, which makes possible the attainment of a considerable size and maturity at the time of hatching in consequence of which the larvæ are better able to take care of themselves. A second condition insuring the success of the offspring is seen in the internal fertilization which insures the impregnation and development of every egg which is deposited. In fact, my experiments have shown that gravid females which are isolated from the males early in the spring and thus fail to become fertilized, do not deposit their eggs at all, and that by the middle of August the eggs are already undergoing rapid resorption.

This fact shows an extreme illustration of the conservation of material in this species, and is quite in line with the conservation shown in the reduction of the number of eggs. It shows a decided advance in comparison with the habits of certain other amphibians such as *Cryptobranchus allegheniensis*, for example, which is prodigal in its egg production, but often uses its own eggs as food (Smith, '07). Finally, it is certain that a most potent contributory factor to the high percentage of success in the development of the offspring of *Desmognathus fusca* is found in the extraordinary constancy and devotion of the mother to her offspring during the incubation period, a devotion no less effective because it is an automatic response.

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